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5 Long and Nelson · Home Range and Dynamic Time Geography

6 **Home Range and Habitat Analysis using Dynamic Time Geography**

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**ABSTRACT** Wildlife home ranges continue to be a common spatial unit for modeling animal habitat selection. Telemetry data are increasing in spatial and temporal detail and new methods are being developed to incorporate fine resolution data into home range delineation. We extended a previously developed home range estimation technique that incorporates theory from time geography, the potential path area (PPA) home range, to allow the home range to be defined at multiple spatial scales depending on the observed rate of movement within the data. The benefits of this approach are demonstrated with a simulation study, which uses multi-state correlated random walks to represent dynamic movement phases to compare the modified PPA home range technique with a suite of other home range estimation methods (PPA home range, kernel density estimation, Brownian bridges, and dynamic Brownian bridges). We used a case study on caribou (*Rangifer tarandus*) movement from northern Canada to highlight the value of this approach for characterizing habitat conditions associated with wildlife habitat analysis. We used a simple habitat covariate, percent forest cover, to explore the potential for misleading habitat estimates when home ranges do not include potentially visited locations (omission area) or include areas not possibly visited (commission area). We highlight the advantages of the dynamic PPA home range in the context of quantifying omission and commission areas in other home range techniques. Finally, we provide our R code for calculating dynamic PPA home range estimates.

**KEY WORDS** caribou (*Rangifer tarandus*), commission area, correlated random walk, omission area, telemetry.

32 With continued development of spatial tracking technologies (e.g., global positioning system [GPS],  
33 Argos), unprecedented datasets are facilitating novel research on wildlife movement and behavior.  
34 These improvements have resulted in wildlife telemetry data with finer sampling intervals, over longer  
35 temporal extents, and with better spatial accuracy (Cagnacci et al. 2010). Improved spatial and  
36 temporal resolution of telemetry data have provided scientists the opportunity to conduct increasingly  
37 detailed analysis of animal movement and the potential to answer increasingly sophisticated questions  
38 regarding wildlife biology, behavior, and response to change (Patterson et al. 2008).

39 The home range continues to be a primary spatial unit for wildlife analysis and modeling (Beyer  
40 et al. 2010). The most oft-cited definition of a home range is the area to which an animal confines its  
41 normal movements (Burt 1943). However, a robust mathematical formulation of this definition is still  
42 absent, and the practical definition of a home range is dependent on the chosen method for estimating it  
43 (Fieberg and Börger 2012). Thus, there are many approaches for estimating wildlife home ranges, for  
44 example minimum convex polygons, kernel density estimation (Worton 1989), local convex hulls (Getz  
45 and Wilmers 2004), and Brownian bridges (Horne et al. 2007).

46 Home ranges are a useful summary unit for spatial analysis of wildlife movement because they  
47 explicitly relate to processes (such as territoriality, spatial memory, and habitat preference) associated  
48 with space-selection patterns in many wildlife species (Börger et al. 2008, Van Moorter et al. 2009). As  
49 a conservation tool, home ranges represent a useful spatial unit for management decision-making and  
50 analysis (Reynolds et al. 1992, Bull and Holthausen 1993, Linnell et al. 2001). Home ranges are  
51 commonly used in 2 areas of spatial analysis: to quantify differences in home range areas and to study  
52 habitat selection. Quantifying differences in home range areas, for example between sexes (Swihart and  
53 Slade 1989), or over time (Smulders et al. 2012) provides insight into wildlife movement processes  
54 associated with spatial selection and mobility. Habitat analysis using home ranges links spatial  
55 selection to underlying environmental covariates and habitat types being used by the individual.

Analyzing changes in home range estimates, or the habitat variables associated with them, is complicated by the presence of areas of omission and commission error. Omission and commission areas are defined, respectively, as habitat used by the animal that is excluded from the home range and habitat that is unused but included in the home range (Sanderson 1966). Similarly, Getz and Wilmer (2004) refer to Type I error as including invalid areas and Type II error as excluding valid areas in home range estimates. Home range estimation methods that reduce omission and commission areas, or methods that can be used to quantify these areas in existing methods, are necessary to improve wildlife home range studies. However making comparisons across home ranges is difficult with empirical data because there is no truth for comparison and each method places different assumptions on the data.

The potential path area (PPA; Long and Nelson 2012) approach takes an alternative view on home range estimation, one based on a time geographic view of individual movement (Hägerstrand 1970). Within the time geographic framework, movement opportunities are represented using a space-time prism, which is a 3-dimensional (space and time) volume that contains all potential movement paths between 2 known telemetry fix locations (Fig. 1). The space-time prism represents a useful measure for understanding the spatial-temporal constraints on individual movement opportunity (Kwan 1999) and for this reason is commonly referred to as the accessibility space (Kwan 1998). The PPA is the projection of the space-time prism onto the spatial plane, and represents a purely spatial measure of accessibility (Fig. 1). The PPA home range is calculated by recursively computing PPA ellipses for consecutive pairs of telemetry locations, which are then combined (using a spatial union) to estimate the home range (see Long and Nelson 2012). The PPA home range estimate focuses explicitly on the delineation of the accessibility space of the individual, which makes it a useful spatial unit for comparing across methods in the context of omission and commission areas.

The size and shape of the space-time prism, and thus the PPA home range estimate, depends on the time between locations and a mobility parameter  $v_{max}$ , which can be interpreted as a maximum

80 travel velocity. In some cases,  $v_{max}$  may be known based on a fine understanding of organism biology.  
81 In most cases,  $v_{max}$  must be estimated from the telemetry data; for example Long and Nelson (2012)  
82 outline several statistical procedures that can be used to estimate  $v_{max}$ , which are derived from methods  
83 for estimating the upper bound of a distribution given a set of values. With the PPA approach,  $v_{max}$  is a  
84 global parameter applied to the entire telemetry dataset (i.e., all pairs of points). With organisms that  
85 exhibit highly variable mobility levels, PPA home range estimates will overestimate home range area  
86 for periods of lower mobility, leading to increased commission areas, a problem also encountered with  
87 other methods (e.g., from over-smoothing; Gitzen et al. 2006, Downs and Horner 2008). A dynamic  
88  $v_{max}$  parameterization incorporating higher and lower mobility levels will reduce over-estimation of  
89 home range areas associated with low mobility phases, and reduce commission area.

90 Explicitly considering wildlife movement phases is one approach to reducing omission and  
91 commission areas (Kranstauber et al. 2012). Kernel and minimum convex polygon approaches, for  
92 instance, cannot include movement phases because they ignore the temporal component of telemetry  
93 data. Most wildlife species exhibit multiple movement phases, often linked to different behaviors,  
94 resulting in variation in patterns and scales of movement, as well as habitat selection. A number of  
95 robust statistical techniques currently exist that can be used to identify different movement phases  
96 within a telemetry dataset (e.g., latent models: Morales et al. 2004, Jonsen, Flemming and Myers 2005;  
97 change-point analysis: Gurarie et al. 2009). Within each phase, movement parameters should follow a  
98 similar pattern, whereas between phases movement parameters shift dramatically from, for example,  
99 low motion (resting) to high motion (migration) states. To reduce omission and commission areas,  
100 space-time variation associated with different movement phases may be useful for refining home range  
101 estimates, and subsequently, habitat selection studies.

102 We extended the PPA approach by dynamically modeling the mobility parameter ( $v_{max}$ ) so that  
103 variation in mobility, based on observed movement phases is incorporated into home range estimation.

104 We call the extension the dynamic potential path area home range (dynPPA). Using simulated data and  
 105 empirical caribou (*Rangifer tarandus*) telemetry data, we demonstrate how the dynPPA approach  
 106 provides an alternative measure of animal space use and a useful comparison metric among existing  
 107 home range techniques for quantifying omission and commission areas. Finally, we provide an R-based  
 108 toolset for performing dynPPA analysis.

## 109 **METHODS**

### 110 **Dynamic PPA Home Range (dynPPA)**

111 We follow Long and Nelson's (2012) method of estimating  $v_{max}$  from a telemetry dataset of  $n$  fix  
 112 locations for a single individual. Estimates of  $v_{max}$  are a function of the distribution of individual  
 113 segment velocities ( $v_i$ ) given by:

$$114 \quad v_i = \frac{d_i}{t_i} \quad [1]$$

115 where  $d_i$  is the distance and  $t_i$  the time between consecutive fixes. Based on the distribution of the  $v_i$  for  
 116 the entire trajectory,  $v_{max}$  is an upper bound on the  $v_i$ , which can be estimated by several statistical  
 117 estimation techniques (e.g., Robson and Whitlock 1964, van der Watt 1980). For example Long and  
 118 Nelson (2012) suggest the method described by van der Watt (1980) which considers the ordered set of  
 119 the  $v_i$  such that  $v_1 < v_2 < \dots < v_{m-1} < v_m$  and  $m = n - 1$ .

$$120 \quad v_{max} = \left( \frac{k+2}{k+1} \right) v_m - \left( \frac{1}{k+1} \right) v_{m-k} \quad [2]$$

121 where  $1 < k < m$  represents the  $k$ th ordered value of  $v_i$ . We extend the  $v_{max}$  estimation procedure from  
 122 Long and Nelson (2012) to account for behavioral shifts throughout the tracking period. Thus, dynamic  
 123  $v_{max}$  is defined by a similar function:

$$124 \quad v_{max, p} = F(v_{i, p}) \quad [3]$$

125 Where  $v_{max, p}$  is the  $v_{max}$  estimate for the  $p$ th dynamic phase comprising of a subset of the  $n$  telemetry  
 126 fixes and  $F(v_{i, p})$  is a statistical technique (e.g., [2]) for estimating the upper-bound of a distribution

127 applied to the  $v_i$  in phase  $p$ . The phases ( $p$ ) may be from a temporally dynamic moving window, or  
128 associated with discrete behavioral phases. Although we used the technique described in van der Watt  
129 (1980), this approach can be used with other functions for estimating the upper-bound of a distribution.  
130 Importantly, such a dynamic calculation of the PPA (dynPPA) home range estimate allows for  
131 variations in the  $v_{max}$  parameter through time resulting from changes in movement behavior.

132 The construction of the dynPPA home range explicitly considers the movement ability of the  
133 individual animal to delineate their accessibility space throughout the movement trajectory. Thus, by  
134 taking a spatial overlay of the dynPPA and other home range estimators, we define areas included in the  
135 dynPPA home range but not included in home range estimates from other methods as omission area  
136 (Fig. 2); these are areas that were accessible to the animal but not included in the home range estimates  
137 from the other methods. Omission area is prevalent in most methods, and is included in the commonly  
138 accepted definition of a home range (i.e., the occasional sallies described by Burt 1943). Quantifying  
139 commission area is not as straightforward, because all home range estimates are likely to include  
140 locations not actually visited by the animal because of the incomplete nature of telemetry data. We  
141 define areas included in the home range estimates from other methods but not included in the dynPPA  
142 home range as observable-commission areas, which represent areas included in the home range but  
143 outside of the accessibility space of the animal (Fig. 2). Observable-commission areas represent  
144 locations the animal could not possibly have visited given the known fix locations and an upper-bound  
145 on mobility ( $v_{max}$ ). For example, the presence of high-levels of observable-commission area is one of  
146 the main reasons why minimum convex polygons are problematic with irregularly shaped patterns of  
147 animal telemetry data (Harris et al. 1990, Barg et al. 2004). Through the analysis of these spatial  
148 differences, we show how the dynPPA home range method improves upon the original PPA model and  
149 provides a unique and complementary view to home range estimation by explicitly delineating the  
150 accessibility space of an individual animal. The dynPPA approach improves upon the PPA approach by

151 accounting for changes in mobility relating to dynamic movement behavior. Further, dynPPA home  
152 range can be used to evaluate and refine home range estimates from other methods through the  
153 quantification of spatial differences, which we define as omission and observable-commission areas.

#### 154 **Other Home Range Methods**

155 Many methods exist for computing wildlife home ranges; we focus on comparing the original PPA  
156 method, 3 more popular current approaches – kernel density estimation (KDE; Worton 1989),  
157 Brownian bridges (BB; Horne et al. 2007), and dynamic Brownian bridges (dynBB; Kranstauber et al.  
158 2012) – and the new dynPPA approach. With KDE, BB, and dynBB, the home range is a 2-dimensional  
159 projection of the utilization distribution of the animal from which a percent volume contour is extracted  
160 to delineate home range as a polygon. Kernel density estimation relies on the selection of a suitable  
161 kernel bandwidth, which remains a highly contentious issue in home range analysis (Hemson et al.  
162 2005, Fieberg 2007). The Brownian bridge approach models movement as a Brownian diffusion  
163 process anchored on 2 consecutive fixes. The  $n-1$  Brownian bridges are combined to produce the BB  
164 home range, and in this sense it is comparable to the PPA approach. The BB home range requires the  
165 selection of 2 variance parameters, one related to uncertainty in fix locations, and the other termed the  
166 Brownian motion variance, which is related to the mobility of the animal. The Brownian motion  
167 variance parameter is estimated globally from the entire telemetry dataset (of an individual) using a  
168 leave-one-out estimation process (Horne et al. 2007). To generalize the BB approach, Kranstauber et al.  
169 (2012) developed the dynBB, which uses a temporally varying estimate of the Brownian motion  
170 parameter to account for dynamic movement phases.

#### 171 **Simulation Study**

172 We simulated 1,000 correlated random walks (CRW) to compare home range estimation techniques.  
173 Correlated random walks rely on 2 parameters. The first ( $r$ ) governs the level of serial correlation in  
174 turning angles and the second ( $h$ ) is a scaling factor for the step-length distribution. To simulate



dynamic movement behavior, we varied the number of distinct movement phases ( $p$ ) within each simulated CRW between 5 and 10. For each movement phase, CRW parameters were chosen randomly but restricted in such a way that higher mobility phases ( $h = 3$  to 5) were associated with more directed (i.e., correlated) movements ( $r = 0.3$  to 0.7), and lower mobility phases ( $h = 1$  to 3) were associated with more random movements ( $r = 0$  to 0.4).

For each simulated CRW, we computed the potential path area home range (PPA), the 95% volume contour kernel density home range estimate, the 99% volume contour Brownian bridge home range, the 99% volume contour dynamic Brownian bridge home range, and the dynamic PPA home range. We computed kernel bandwidth for KDE using the half the reference bandwidth, a modification that can reduce the effect of over-smoothing in KDE when data exhibits clumpy patterns (Worton 1995). We selected the 95% volume contour because it is the most commonly chosen level in past home range studies (Laver and Kelly 2008) and is typically used to estimate the home range, whereas lower values (e.g., 50%) are used to delineate core area. We computed the variance parameter for the BB and dynBB models using the maximum likelihood method outlined by Horne et al. (2007) and assumed the error parameter to be appropriately small. We chose a 99% volume contour level for the BB and dynBB methods following Horne et al. (2007).

For each technique, we computed the home range area, plus the intersection area with the dynPPA to examine spatial differences among methods. Results from the simulated study are presented as percentages of the dynPPA for comparison purposes, thus making the area of the dynPPA home range estimate the baseline areal measurement.

### **Case Study – Caribou in Northern British Columbia, Canada**

To further demonstrate the dynPPA approach, we used a dataset of the movements of 4 caribou over the course of a year (2001). The telemetry data were collected with a regular, 4-hour sampling interval, with < 5% fixes missing. Unlike the simulation examples, in telemetry studies the number and duration

of movement phases are generally unknown. We use the behavioral change point algorithm (BCPA: Gurarie et al. 2009) to identify different movement phases for each individual caribou. The BCPA requires 2 parameters. The first is the BCPA search window ( $w$ ; Gurarie et al. [2009] suggest  $w > 30$ ); we used  $w = 43$ , approximately a 1-week interval in this example. The second parameter is a threshold that identifies significant change points; we used 21, which is half of  $w$ , similar to that used by Gurarie et al. (2009). We then computed the PPA, KDE, BB, dynBB, and dynPPA home ranges following the methods for parameter estimation outlined in the simulation study. We again explore the presence of omission and observable-commission area in various home range techniques in the caribou example through area overlap comparisons with dynPPA.

We estimated the habitat composition (i.e., land cover) for each home range based on each home range estimation method to examine the effect of method on the composition estimates. To represent land cover, we used the Canada's Earth Observation for Sustainable Development (EOSD) dataset (Wulder et al. 2008), which was derived from Landsat satellite imagery. We selected percent forest cover as an indicator of habitat because wooded areas are a primary habitat type for caribou, especially outside of summer months (Wood 1994, Seip 1998). We focus on the percent forest cover within each home range along with the sub-areas of the home range delineated as omission area and observable-commission area to examine whether the composition of these sub-areas differed from the overall home range, resulting in misleading composition estimates from home range methods.

## **RESULTS**

### **Simulation Study**

Our simulations revealed differences between estimated home range areas and the presence of omission and observable-commission area across different home range methods (Fig. 3). The PPA approach produced larger estimated home range sizes, as expected, whereas the BB and dynBB methods produced smaller home range estimates than dynPPA. Kernel density estimation produced home range

estimates that could be either larger or smaller than dynPPA (Fig. 3). Omission area was greatest in the BB and dynBB methods, but this is expected because these methods produced the smallest home range estimates. In many situations, KDE also produced a substantial level of omission area, which is surprising given that in general KDE produced the largest home range size estimates. As expected based on definitions, omission area in the PPA was 0 because the PPA home range contains the dynPPA home range.

In all simulations, PPA and KDE produced an observable-commission area (Fig. 3). Of these, 790/1,000 of the simulation PPA home ranges and 975/1,000 of the simulation KDE home ranges contained observable-commission area comprising greater than 10.0% of the estimated home range. The average percentage of observable-commission area was highest in KDE at 36.2%, with an average of 14.6% for PPA. The BB and dynBB methods also produced some level of observable-commission area in nearly all simulations (998/1,000 and 997/1,000 simulations, respectively). However, neither method produced a simulation where the amount of observable-commission area was greater than 10% proportionally of the home range area. The average observable-commission area was small in BB and dynBB (1.2% and 0.7%, respectively). Overall, BB and dynBB compare best with dynPPA, likely owing to similar derivations based on the sequence of telemetry fixes (path-based), producing similar sizes and minimizing observable-commission area.

#### **Case Study – Caribou in Northern British Columbia, Canada**

The 4 caribou in northern British Columbia, whose data we analyzed, exhibited similar movement patterns consisting of 2 spatially disjoint seasonal ranges connected via movement corridors (Fig. 4). Estimated home range areas had similar patterns as seen in the simulation study, with larger estimated home ranges from the PPA and KDE methods, and smaller estimated home ranges from the BB and dynBB methods (Fig. 4). Kernel density estimation produced the largest estimated home ranges but also produced estimates that differed in shape and structure from the path-based methods.

With the caribou dataset, the trend in estimated home range areas showed PPA or KDE being largest, followed by dynPPA, BB, and dynBB (Fig. 5). In the case of caribou C4, the KDE home range estimate was much larger owing to difficulty in specifying a suitable bandwidth using the objective method chosen. The dynBB and BB methods are excellent at minimizing observable-commission areas, and produce estimated home range sizes similar to each other. The KDE and PPA approaches both produced substantial areas of observable-commission area, which is problematic in home range studies because these areas are outside of the defined accessibility space of the animal.

Estimated habitat composition revealed the potentially misleading effect of observable-commission areas (Fig. 6). For example, with the KDE method with data from caribou C2, the observable-commission area was a substantial portion of the estimated home range, and the percent forest cover was relatively high for this area. The high percent forest cover in the observable commission area portion of the home range in C2 resulted in the highest observed percent forest cover of all the home range methods, noticeably higher than any other estimates (Fig. 6). Conversely, in caribou C4, the percent forest cover was similar in the observable-commission area to that of the dynPPA home range, in this case leading to equivalent measures of percent forest cover, despite the substantial overlap of home range size by the KDE method. The BB and dynBB methods produced relatively small areas of observable-commission area, despite having substantial differences in percent forest cover between the home range and observable-commission areas. However, in caribou C3, estimates for percent forest cover were lower for the BB and dynBB methods because the omission area had a higher percent forest cover, which shows the potentially misleading effect of omission area.

## **DISCUSSION**

Concepts from time geography can be used to explicitly consider the elapsed time between telemetry fixes, allowing home range estimation to use a path-based data representation (Long and Nelson 2012). Traditionally, home range estimation techniques borrowed from computational geometry or statistics,

271 are point-based approaches, and define an enclosure or smooth a set of telemetry fixes. Point-based  
272 methods use only the spatial geometry of telemetry fixes and thus may be hindered by the serially  
273 correlated structure of modern telemetry datasets (Dray et al. 2010). Path-based methods for estimating  
274 the home range leverage the temporal structure inherent in telemetry datasets. For example, methods  
275 may consider consecutive telemetry fixes as anchor points in a diffusion (Brownian bridge) or  
276 diffusion-drift process (biased random bridge; Benhamou 2011). The Brownian bridge and biased  
277 random bridge methods delineate the utilization distribution of an individual based on random walk  
278 theory, whereas the dynPPA home range method focuses on quantifying the polygon area accessible to  
279 an individual given  $n$  telemetry fixes and a time-varying mobility parameter.

280         The dynPPA method takes an alternative view on estimating the home range, one that explicitly  
281 considers that accessibility can be used to directly estimate the home range. That is, the dynPPA  
282 delineates the area an animal could have visited based on a set of telemetry fixes and a time varying  
283 mobility parameter  $v_{max}$ . We have demonstrated that dynPPA home range estimates can provide useful  
284 stand-alone measures for estimating home range areas, comparable with popular existing methods. We  
285 highlight the dynPPA approach as being simple and intuitive, but also stress how it can be used to  
286 identify omission and observable-commission areas when comparing across multiple methods, a  
287 practice increasingly common given the ease at which multiple methods can be implemented within a  
288 single software (e.g., Calenge 2006). Specifically, because the dynPPA home range estimate focuses on  
289 accessibility in its definition, we demonstrate how dynPPA can be used to quantify omission and  
290 observable-commission area in other estimation techniques. Such comparisons are conditional on the  
291 predication that the dynPPA estimate, which defines the individual accessibility space, represents a  
292 suitable baseline for identifying omission and observable-commission area.

293         Wildlife researchers now have an array of computational tools from which to choose for  
294 carrying out sophisticated spatial-temporal analyses on wildlife telemetry datasets. However, there

295 remains a need to define relatively straightforward spatial analysis units, drawing on the foundational  
296 concept of the home range. The dynPPA home range method is based on different assumptions from  
297 other home range approaches. We propose that because dynPPA explicitly considers accessibility in its  
298 definition, it can be used for quantifying omission and observable-commission areas through direct  
299 spatial comparisons of home range polygons. Further, many studies are interested in studying habitat  
300 use versus habitat availability from telemetry data (Beyer et al. 2010). In use versus availability study  
301 designs, the researcher must carefully consider how they define available habitat. At some scales, a  
302 home range estimate (or a spatial extension of the home range such as a buffer around the home range)  
303 is used to define potentially available habitat (Long et al. 2010). A time geographic approach (i.e.,  
304 dynPPA) is a logical method for identifying what constitutes available habitat in use versus availability  
305 studies because dynPPA explicitly delineates accessible areas.

306       Our simulation study highlights the challenges with home range analyses that researchers have  
307 been grappling with for decades: that different home range methods can lead to highly variable  
308 estimates of home range size and configuration. When compared to other home range estimation  
309 methods, dynPPA is generally larger than produced by BB or dynBB methods but smaller than for KDE  
310 and the original PPA approach. From comparisons between home range estimates from other methods  
311 with dynPPA, a researcher can decide whether a home range method is appropriate with a given  
312 dataset, or re-evaluate the chosen parameter combinations. Our simulations can also be seen as further  
313 evidence of the difficulty with KDE home range methods or more specifically the problem of  
314 automated selection of the bandwidth (Hemson et al. 2005). In the simulation study, we use a popular  
315 ad hoc method for identifying the kernel bandwidth (i.e., half the reference bandwidth), but the  
316 resulting home range estimates were highly variable in size. When the home range is overestimated, the  
317 result is substantial observable-commission area, which can be problematic when using home ranges  
318 for habitat composition analysis.

319       The results (both from the simulations and caribou study) confirmed that, like many home range  
320 estimation methods, the original PPA approach (Long and Nelson 2012) may be overestimating home  
321 range areas. We built on the ideas proposed by Kranstauber et al. (2012), that home range estimation  
322 methods should consider different movement phases associated with variable movement parameters.  
323 Thus, dynPPA is a generalization of the original PPA approach, where  $v_{max}$  is estimated independently  
324 for each movement phase. This approach considers movement phases as discrete segments along the  
325 trajectory, such that changes in movement parameters occur abruptly between phases (Kranstauber et  
326 al. 2012) and typically represent a change in movement behavior (e.g., migrating vs. foraging).  
327 Alternatively, movement parameters may vary continuously over time, and we have also implemented  
328 a temporal moving-window approach for estimating  $v_{max}$  dynamically over time. We did not evaluate  
329 the temporal moving-window method here but make it available with the R code provided to allow  
330 researchers to use a moving-window approach should it be appropriate with their research (see  
331 Supporting Information).

332       Methods for estimating movement parameters are complicated by missing fixes and irregular  
333 fix intervals (see Laube and Purves 2011), issues commonly encountered in empirical wildlife  
334 telemetry studies. Shorter than average fix intervals may be associated with higher segment velocities  
335 ( $v_i$ ), which would be unrealistic with longer fix intervals. Many tracking devices are programmed to  
336 obtain fixes at specific intervals, which if they fail, continue to re-attempt fixes until successful. This  
337 can result in fixes that were programmed at regular intervals being collected at irregular intervals, some  
338 of which may be relatively short. If these short fix intervals are associated with a burst of movement, a  
339 relatively high  $v_{max}$  estimate will result, which will be inappropriate with longer intervals. Also, many  
340 modern telemetry studies are programming wildlife tracking devices to vary the tracking interval  
341 depending on time of day (e.g., 15-min tracking interval during the day and 2-hr interval at night). In  
342 such cases, estimates of  $v_{max}$  associated with the shorter interval would not reflect the estimates during

343 the 2-hour period. Such discrepancies are due to the fact that animals are limited in their ability to  
344 maintain faster movement speeds over longer time intervals. When unrealistically high  $v_i$  values are  
345 included in the distribution of the  $v_i$ , it will become positively-skewed, and the  $v_{max}$  parameter will be  
346 overestimated. Overestimation of  $v_{max}$  results in a home range area that is unexpectedly large when  
347 using the dynPPA approach. A similar process occurs with other home range techniques, such as when  
348 the bandwidth (in kernel density estimation) or the variance parameter (in Brownian bridge models) is  
349 overestimated. When using the dynPPA home range method on wildlife datasets with irregular or  
350 missing fixes, the over-estimation of  $v_{max}$  can be reduced by examining the skewness of the  $v_i$   
351 distribution and analyzing those segments above a chosen threshold independently. Long and Nelson  
352 (2012) suggested that the PPA approach was useful only with relatively dense and regularly sampled  
353 telemetry data. However, dynPPA is more suitable with irregular tracking schemes because the tracking  
354 interval can be directly related to movement phases (e.g.,  $p$  in [3]) in the calculation of  $v_{max}$ . However,  
355 more research is needed to study the effect of variable and missing data on the  $v_{max}$  estimation  
356 procedure associated with dynPPA home range estimates.

357 Wildlife exhibit different movement phases associated with different movement behaviors (e.g.,  
358 migration, foraging, searching). Distinct movement phases result in different movement patterns, and  
359 thus influence the patterns observed in telemetry data from wildlife tracking systems. Mathematical  
360 models for examining variations in animal movement behavior have become increasingly sophisticated  
361 and provide novel insights into fine-scale variations in animal behavior (Langrock et al. 2012,  
362 McClintock et al. 2012). However, methods incorporating dynamic behavior into analysis of wildlife  
363 space use (i.e., home range analysis) remain limited. The inclusion of changing behavior in wildlife  
364 movement models and spatial analysis is essential for improving space-use estimates (Kranstauber et  
365 al. 2012), and the subsequent analysis of underlying environmental variables. The dynPPA represents a  
366 new approach that can easily incorporate animal movement behavior phases, estimated via robust



367 statistical models, directly into the home range estimation procedure.

368         Each technique for home range estimation is based on unique methods and assumptions and as a  
369 result is likely to produce different home range shapes and sizes (Fieberg and Börger 2012). Variation  
370 between methods has led many authors to compare across home range methods (Huck et al. 2008),  
371 often to highlight the deficiencies in existing approaches in specific scenarios (Downs and Horner  
372 2008). The difficulty in selecting a method for home range estimation, especially with empirical data, is  
373 that there is no truth. Our comparisons, across 5 home range estimation methods, emphasize the unique  
374 information content of each method and how these approaches can be chosen based on research  
375 questions and the nature (i.e., resolution and extent) of the data from which the home range is to be  
376 estimated (Fieberg and Börger 2012, Powell and Mitchell 2012). When research questions emphasize  
377 accessibility (in space and time), dynPPA represents an appropriate home range estimator, given  
378 relatively high-resolution telemetry data. The concept of accessibility is useful when researchers wish  
379 to study whether animals have the potential to interact with features on the landscape (e.g., well sites,  
380 Sawyer et al. 2006, or roads, Long et al. 2010). With other research questions or data types, other home  
381 range estimation techniques may be more appropriate. For example, with coarse tracking data  
382 associated with satellite very high frequency (VHF) radio collars where serial correlation is lower,  
383 KDE methods are more appropriate. With animals that exhibit compact and regular shaped territories,  
384 simpler methods, such as minimum convex polygons, may be sufficient for estimating home range size  
385 and shape (Downs and Horner 2008). Further, when comparisons among multiple home range  
386 estimates are being made, in either an exploratory or analytical stage, we demonstrate the value of  
387 including the dynPPA method, where appropriate, because dynPPA can serve as a baseline from which  
388 to quantify omission and observable-commission area.

## 389 **MANAGEMENT IMPLICATIONS**

390 Home ranges are a typical spatial unit for conservation. The presence of omission and observable-

commission areas in home range estimation and subsequent habitat analysis can be misleading. In an era of increasing geographical pressures on conservation activities, tools such as the dynPPA home range can assist in the conservation of wildlife by refining spatial estimates of home range. Simply, the dynPPA home range method can be used to assess if areas within a home range were accessible to an animal given spatial-temporal constraints. We provide some guidelines for conducting home range analysis using dynPPA and further demonstrate how to use dynPPA to investigate omission and observable-commission area in comparisons with other home range methods. Home ranges containing substantial omission or observable-commission areas should be used with caution because they may misrepresent the size of the home range, which can result in misleading habitat analyses. By carefully considering the presence of omission and observable-commission area in home range estimates, wildlife managers can improve the geographic focus of conservation efforts. Finally, we provide a free and open tool for computing the dynPPA, in the statistical software R, to make the calculation of dynPPA available to other researchers.

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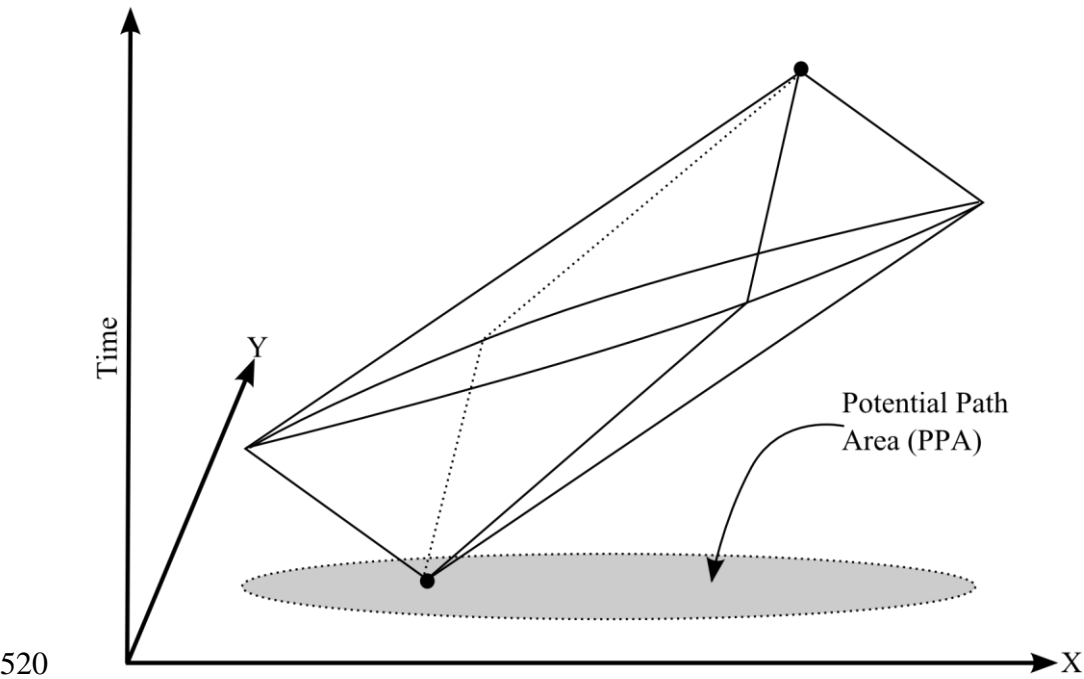
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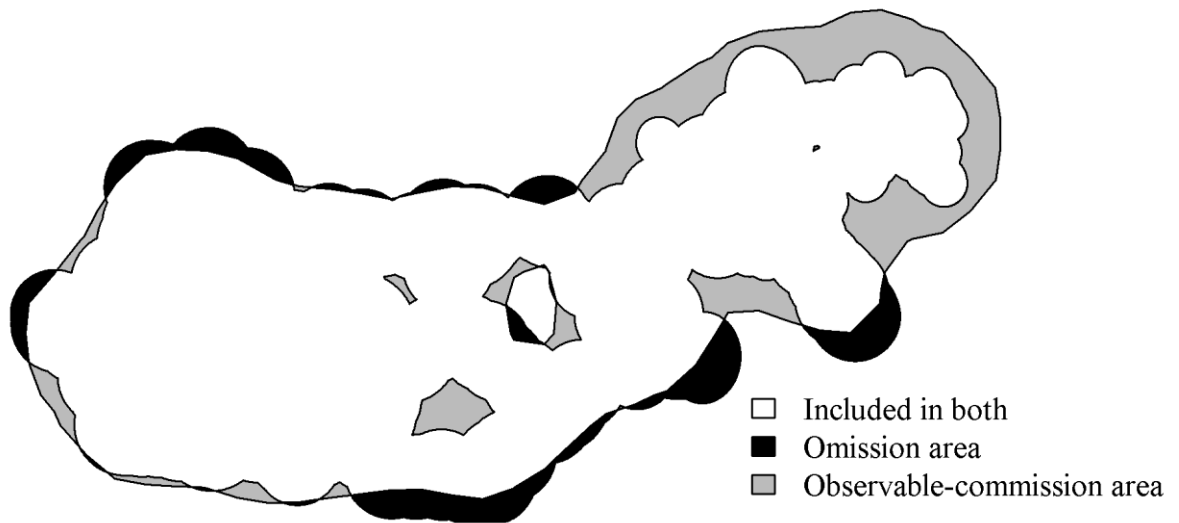
519 **FIGURE CAPTIONS**



521 Figure 1. The space-time prism from time geography that delineates the accessibility space for  
522 movement between 2 constraint fixes, based on a known mobility parameter ( $v_{max}$ ), which controls the  
523 size of the prism. The potential path area (PPA) is the projection of the space-time prism onto the  
524 spatial plane, and geometrically can be represented as an ellipse.

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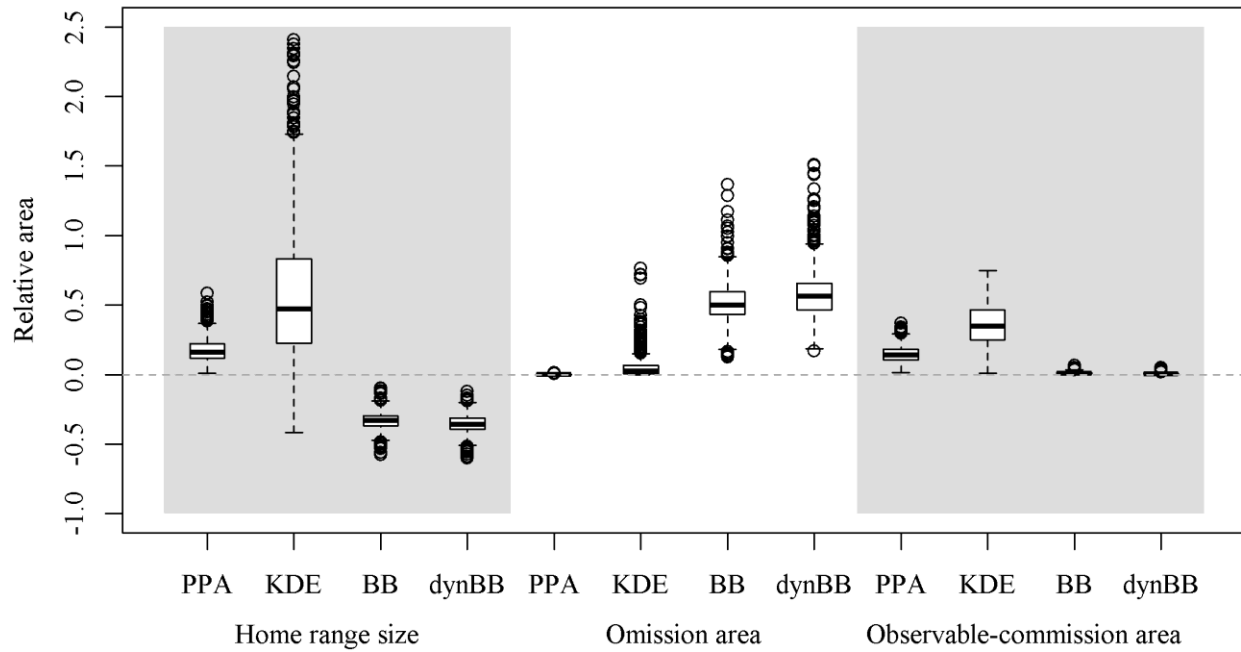


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527 Figure 2. Comparison of a typical home range, with a dynamic potential path area (PPA) home range

528 demonstrating how omission and observable-commission areas can be quantified and mapped.

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Figure 3. Boxplots showing the relative area of the potential path area (PPA), kernel density estimate (KDE), Brownian bridge (BB), and dynamic Brownian bridge (dynBB) home range estimation methods in comparison to the dynamic potential path area (dynPPA) method (panel 1), the amount of omission area in each method relative to the area of the individual home range (panel 2), and the amount of observable-commission area in each method relative to the area of the individual home range (panel 3). The median line is located within the boxes that delineate the interquartile range (25<sup>th</sup> and 75<sup>th</sup> percentiles) of the data. Whiskers extend to 1.5 the interquartile range, with outliers plotted as points.

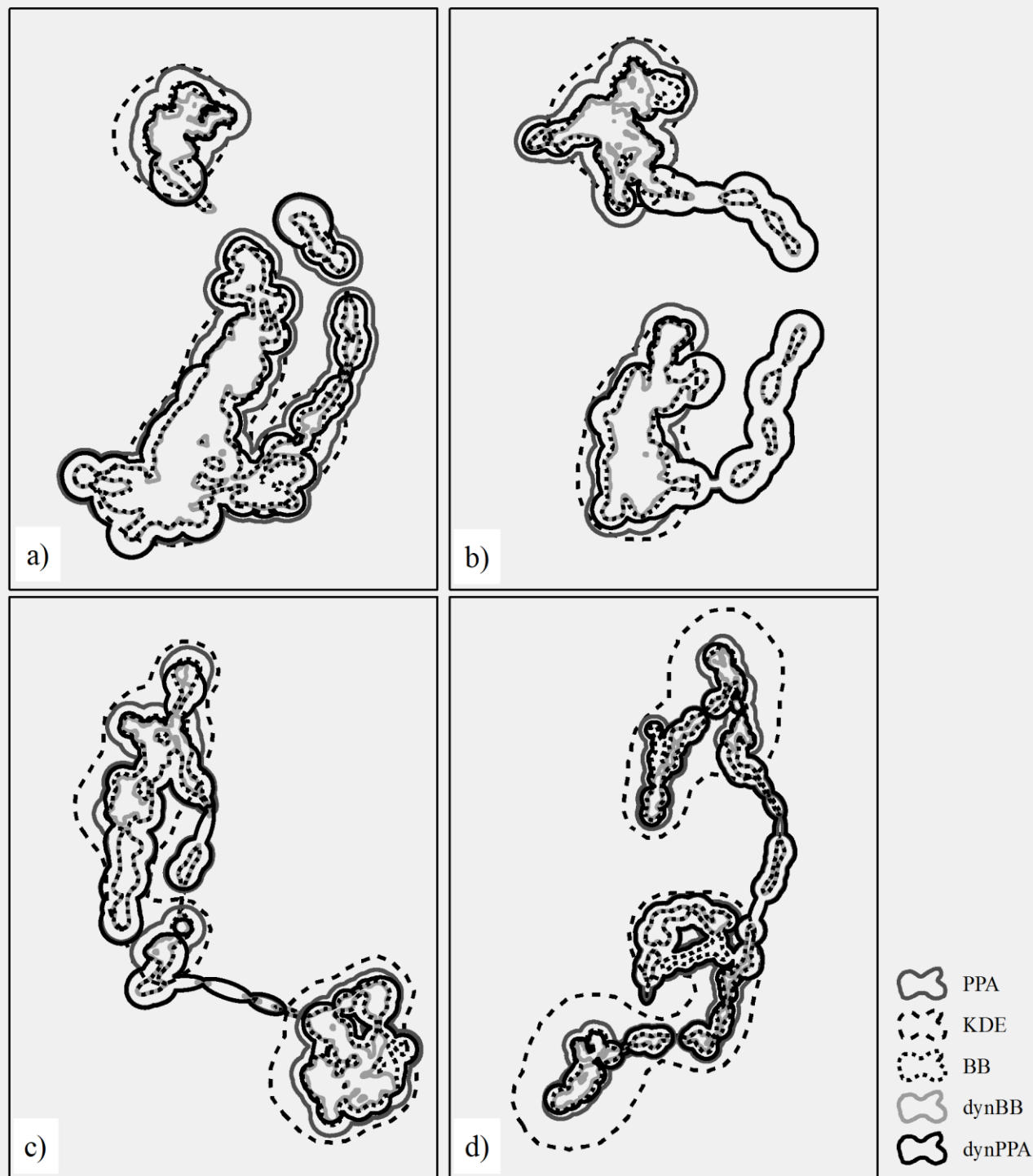
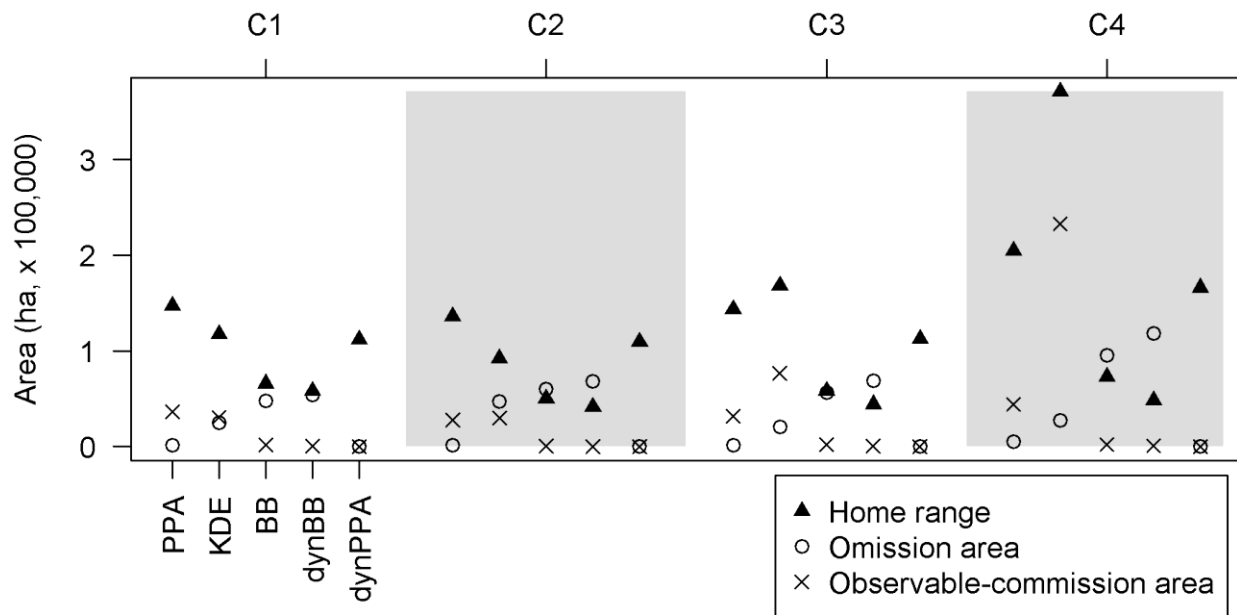


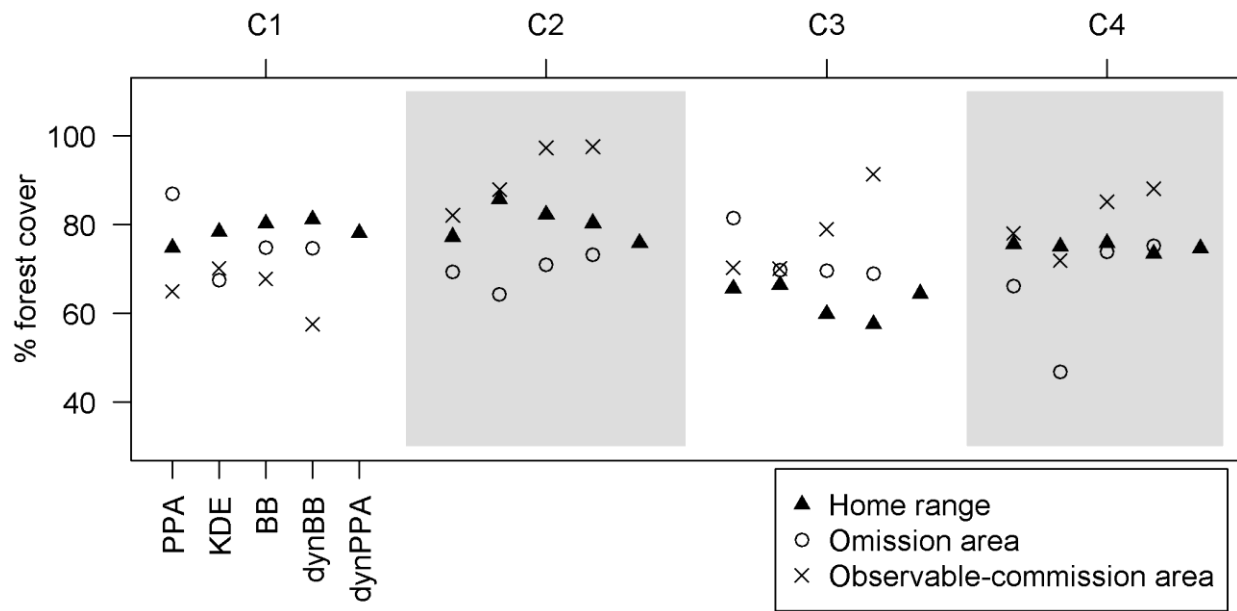
Figure 4. The potential path area (PPA), kernel density estimate (KDE), Brownian bridge (BB), and dynamic Brownian bridge (dynBB), and dynamic potential path area (dynPPA) home range estimates for each of 4 caribou: a) caribou C1, b) caribou C2, c) caribou C3, and d) caribou C4.



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546 Figure 5. The potential path area (PPA), kernel density estimate (KDE), Brownian bridge (BB), and  
 547 dynamic Brownian bridge (dynBB), and dynamic potential path area (dynPPA) home range areas for  
 548 each of 4 caribou (C1, C2, C3, and C4) compared, along with the area of omission and observable-  
 549 commission area for each home range method.

550



551

552 Figure 6. Percent forest cover within the potential path area (PPA), kernel density estimate (KDE),

553 Brownian bridge (BB), and dynamic Brownian bridge (dynBB), and dynamic potential path area

554 (dynPPA) home ranges for each of 4 caribou (C1, C2, C3, and C4), along with the percent forest cover

555 within the omission and observable-commission areas within each home range.

556